SPIDER FAUNA OF SUGAR MAPLE AND WHITE ASH IN NORTHERN AND CENTRAL NEW YORK STATE

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ABSTRACT.   The purpose of this study was to identify spiders associated with foliage of sugar maple, *Acer saccharum* Marsh. and white ash, *Fraxinus americana* L., and to investigate their distribution and relative abundance within the crowns of these two northern hardwoods. Spiders were collected during June through August 1995 from the lower and mid-crowns of ten dominant/codominant sugar maples, five white ash and understory sapling and herbaceous foliage ≤2 m from the ground in a northern hardwood stand in Cortland County New York. These samples were compared for differences in species composition and density (number/25 leaf-clusters; number/100 g dry leaf weight). The spider fauna obtained from this intensive sample was compared to that of an extensive, 20-year survey from the mid-crown of sugar maple in 15 northern hardwood stands in northern New York (St. Lawrence and Lewis Counties). The intensive overstory collection (1995) from maple provided 694 specimens (7 families, 11 genera, 13 species). The dominant families were Philodromidae (43%) and Theridiidae (26%). The most abundant species were *Philodromus rufus* Walckenaer 1826 and *Enoplognatha ovata* (Clerck 1757). Sugar maple averaged 2.6 ± 0.6 spiders/25 leaf-clusters and 14.2 ± 0.6/100 g of foliage. Density of dominant taxa and total numbers did not differ significantly ($\alpha = 0.05$) between crown positions. Significantly fewer hunters/100 g leaf weight occurred on the distal half of mid-crown branches compared to the basal half. Hunters were the dominant foraging guild in terms of both numbers (65%) and number/100 g leaf weight (56%). One hundred twenty four specimens were obtained from white ash (7 families, 9 genera, 9 species). Density on ash averaged 2.6 ± 1.3/100 g leaf weight and *P. rufus* and *Araniella displicata* (Hentz 1847) were the most abundant species. Significantly fewer spiders occurred on white ash compared to sugar maple (14.2 ± 0.6/100 g of foliage. The extensive sample provided 712 specimens consisting of 12 families, 27 genera and 40 species. The most abundant species recovered was *Pelegrina proterva* (Walckenaer 1837). The web spinner, *E. ovata* was the most common species recovered from understory foliage (96% of 763 specimens).

Keywords: Spider diversity, community structure, biodiversity

Sugar maple, *Acer saccharum* Marsh., is important to the ecology and economic value of many northern hardwood forests. In recent decades, its abundance has steadily increased relative to associated species in this forest type (Allen 1996), most likely due to its silvical characteristics (Godman et al. 1990) and forest management practices (Nyland 1992). The major defoliators of sugar maple (Houston et al. 1990; Martineau 1984) and their insect parasitoids and predators (e.g., Allen 1972, 1976a, 1979; Côté & Allen 1973) are well known, but only two studies have examined the spider fauna on this tree species

or in a northern hardwood forest where it was a major component. These arachnids are potential natural control agents. The first step in elucidating their significance in this respect is to identify the species present in tree crowns and determine their relative abundance. Uetz and Dillery (1969) collected spiders in a residential area of Albion, Michigan from the lower crowns of sugar maple during the fall. Throughout the growing season of 1961 through 1964, Drew (1967) sampled for spiders in the herb-shrub and leaf litter strata of a beech-maple forest on Beaver Island, Michigan.

The primary objective of this study was to identify the arboreal spiders associated with sugar maple sampled in northern New York State (St. Lawrence and Lewis Counties) an-

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nually from 1975 through 1995 and compare these species and their relative densities with those recovered in an intensive, one-year (1995) sample in a central region of the state (Cortland County). Secondary objectives were: to determine if spider fauna and spider density varied with crown position in sugar maple and white ash, *Fraxinus americana* L., a common associate of maple in northern hardwood forests; to compare the species composition of the spider community on understory foliage with that found in overstory crowns and to determine the relative abundance of web spinning and hunting spiders in these habitats.

METHODS

From June–August 1995, sampling for spiders in north-central New York took place at Heiberg Forest (Cortland County), a property of the State University College of Environmental Science and Forestry. The site encompassed approximately one hectare and the overstory was predominantly sugar maple, with white ash as a secondary species. The stand also contained black cherry (*Prunus serotina* Ehrh.), quaking aspen (*Populus tremuloides* Michx.) and red maple (*A. rubrum* L.).

Understory vegetation comprised mainly sugar maple and white ash regeneration, along with scattered red maple, Virginia creeper (*Parthenocissus quinquefolia* Planch.), poison ivy (*Rhus radicans* L.), blue cohosh (*Caulophyllum thalictroides* (L.) Michx.), trillium (*Trillium* sp.), thistles (*Cirsium* sp.), touch-me-not (*Impatiens* sp.) and asters (*Aster* sp.). The soil at this site is classified as Mardin channery silt loam, medium-textured, strongly acidic and moderately well drained (Seay 1961).

Spiders were collected from northeast and southwest quadrants of the lower and middle third of the crowns (foliated portion) of ten sugar maples. Sample trees had a mean diameter at breast height (dbh = diameter at 1.4 m from the ground) of 46.4 ± 1.1 cm (SE) and a mean height of 22.4 ± 1.1 m and five white ash (mean dbh = 20.7 ± 2.4 cm; mean height. = 17.4 ± 2.3 m). Samples were distributed in this manner to determine if spider density varied with crown position. It was assumed the two aspects and two crown levels sampled represented habitats where relevant differences in temperature and humidity were

likely to occur which, in turn, may have influenced spider distribution (Pointing 1966). Two branches were removed from each sampled quadrant and crown level. Each branch was then divided into distal and basal halves, each half was bagged separately and brought to the laboratory for processing. Therefore, there were 160 sample units for sugar maple (2 aspects × 2 crown levels × 2 branches × 2 branch sections × 10 trees) and 80 sample units for white ash (2 aspects × 2 crown levels × 2 branches × 2 branch sections × 5 trees). Sample branches were selected arbitrarily, cut at the base with a hand saw and carefully lowered onto a drop cloth. The following information was obtained for each branch section: length (m), basal diameter (cm), number of leaves, dry leaf weight (g), number of leaf-clusters (sugar maple only) and number of spiders.

Within a crown level, spider numbers from both quadrants (NE, SW) were averaged to compensate for possible variation associated with spider movements due to diurnal fluctuation of physical variables (Pointing 1966) or prey movement (Nyffeler et al. 1994). Spider densities for each sugar maple branch section (distal half, basal half) were recorded as numbers per 25 leaf-clusters to weight samples for differences in foliage quantities. For both sugar maple and white ash, spider densities were also expressed as numbers per 100 g of dry leaf weight. This compensated for differences in foliage biomass and facilitated comparison of spider densities between the two tree species.

Spiders were hand collected from the understory by starting at one end of the site, walking in a straight line to the opposite side and searching all foliage within 2 m of the ground. At the opposite end of the transect, walking direction was reversed and the site was traversed a second time parallel to the first line. Approximately 100 transects spaced at 1 m intervals were required to examine understory foliage within the 1 hectare site.

Spiders were identified by the senior author using published keys of Comstock (1948) Dondale (1978, 1982) Kaston (1948, 1978) and Levi (1957, 1963); and by using reference collections. Determinations of representative species were confirmed by D.T. Jennings. Most females were identified by external examination of the epigynum; however, for *Pe-*

legrina spp. it was necessary to dissect and examine the internal morphology of this structure. Males were identified by examining palpal morphology. Adult spiders in good condition were identified to species, damaged individuals to family. Recognizable juveniles were identified to species, otherwise they were identified to genus or family. Enumeration of spider taxa follows Platnick (1989, 1993, 1997) and Maddison (1996). The entire collection is housed in the invertebrate museum of the Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, New York.

Both the paired t-test and 2 × 2 factorial ANOVA (α = 0.05) were employed to analyze within-crown distributions of spiders on sugar maple. Data were tested for homogeneity of variances prior to analyses. The G-test (Sokal & Rohlf 1981) was calculated to compare web spinner *vs* hunter (i.e., all non-web spinners) percentages for sugar maple, white ash, and sugar maple in the understory.

The spider fauna collected in north-central New York during 1995 was compared to a 20-year collection (1975–1995) made by D.C. Allen at 15 sites located in two northern counties of the state (St. Lawrence, Lewis). This extensive sample was made in conjunction with annual monitoring of sugar maple foliage for eggs of the saddled prominent, *Heterocampa guttivitta* (Walker) (Lepidoptera, Notodontidae). For these annual samples, a 1.5 m branch tip was removed with aluminum pole-pruners from the mid-crown level (middle third of the foliated portion of the tree; in these stands, 12–15 m above ground) of each of ten dominant or co-dominant trees. Overall sample size was: 1 branch tip/tree × 10 trees/ site × 15 sites/yr. × 20 yrs. = 3000 branches. Additionally, spiders were occasionally collected by hand from the lower crowns (*n* = 58 specimens) of sugar maple. Each year sampling was done during the last week of June or first week of July. Sampled stands represent the northern hardwood forest type; i.e., each consisted of 50% sugar maple, American beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula alleghaniensis* Britton), either singly or in combination (USDA Forest Service 1965). In 1975 tree size (dbh, cm), abundance (trees/ha) of sugar maple and stand density (BA, m²/ha) were similar among all sites

(D.C. Allen, unpubl.). In 1995, stand density averaged 22.0 ± 3.0 (SE) m²/ha, 79% of which was sugar maple (range 35–98%). For six of these stands measured again in 1997, diameter of sugar maple ranged from 30.6 ± 1.6 cm to 41.6 ± 2.4 cm. All stands are second growth, 100–110 years old and have a history of intensive management for wood products or sap production.

For the 20-year study, numbers of spiders are reported as total collected and each species as percent of total spiders collected compared to the 1995 study that focused on spiders per unit of foliage. In most cases spider numbers cannot be compared statistically; however, the spider complex recovered in the 20-year sample provided an opportunity to compare dominant species, genera, and families with material obtained during the more intensive short-term study (1995) in a different geographic location.

RESULTS

Spiders collected from sugar maple in 1995 comprised 694 specimens, representing 7 families, 11 genera and 13 species (Table 1). Only 32 specimens (0.05%) were adults. Principal families were Philodromidae (47%) and Theridiidae (26%). The Clubionidae, Araneidae, Salticidae, Linyphiidae, and Tetragnathidae together accounted for 28% of the collection. Numerically dominant species were *Philodromus rufus* Walckenaer 1826 (47%) and *Enoplognatha ovata* Clerck 1757 (22%). Their dominance based on relative density (spiders/ 100 g of leaf weight) was: *P. rufus* (38%), and *E. ovata* (30%). For example, if there were 14 spiders per 100 g of leaf weight, approximately five (38%) were philodromids.

An average of 2.6 ± 0.6 (SE) spiders/25 leaf-clusters and 14.2 ± 0.6 spiders/100 g of leaf weight occurred on the 160 branch sections from sugar maple. Neither the 2 × 2 factorial ANOVA (Table 2) nor paired *t*-tests revealed significant differences in number of spiders/25 leaf-clusters or number of spiders/ 100 g leaf weight for two sugar maple crown positions (mid-*vs* lower crown), total numbers (both guilds combined), dominant taxa (family, genus and species), or numbers of web spinners. There was a significant ($P = 0.02$) interaction for numbers of hunters/100 g leaf weight in mid-crown distal branch sections; however, the main effects were not significant

Table 1.—Species and numbers of spiders collected from sugar maple at Tully, Cortland County, New York, 1995.

Spider taxa	Number of individuals
Theridiidae	
Enoplognatha ovata (Clerck 1757)	150
Theridion murarium Emerton 1882	12
Theridion sp.	18
(family only)	2
Linyphiidae	
Ceraticelus sp.	5
Neriene sp.	8
Araneidae	
Araneus nordmanni (Thorell 1870)	1
Araneus sp.	10
Araniella displicata (Hentz 1847)	32
Cyclosa conica (Pallas 1772)	1
Tetragnathidae	
Tetragnatha laboriosa Hentz 1850	1
Tetragnatha sp.	1
Clubionidae	
Clubiona canadensis Emerton 1889	94
Clubiona obesa Hentz 1847	3
Clubiona sp.	7
Philodromidae	
Philodromus rufus Walckenaer 1826	296
Philodromus vulgaris (Hentz 1847)	26
Philodromus sp.	1
Salticidae	
Pelegrina proterva (Walckenaer 1837)	2
Pelegrina sp.	24
Total	694

(mid- *vs* lower crown, $P = 0.31$; and basal *vs* distal branch sections, $P = 0.43$). Spiders/100 g of leaf weight and spiders/25 leaf-clusters were highly correlated (Pearson-Product Moment) with each other for both web spinners ($r = 0.99$) and hunters ($r = 0.97$). The crown level-branch position interaction for hunting spiders/25 leaf-clusters was close to significance ($P = 0.06$), and the correlation between crown level and aspect was very high ($r = 0.97$). For the mid-crown level of sugar maple, significantly ($P = 0.06$, Table 2) fewer hunters/100 g leaf weight occurred on distal branch sections (mean = 3.0 ± 1.7) compared to basal sections (10.5 ± 3.2) (Table 3). Conversely, density of web spinners was similar between branch positions within both crown levels (Table 3). Hunters were the dominant

foraging guild based on total spiders (65%) and on spiders/100 g of leaf weight (56%). Understory samples produced 763 specimens (98% juveniles) representing the Theridiidae, *Enoplognatha ovata* (Clerck 1757), $n = 737$; *Theridion* sp., $n = 2$; Araneidae, *Araniella displicata* (Hentz 1847), $n = 2$; *Cyclosa conica* (Pallas 1772), $n = 14$; Clubionidae, *Clubiona obesai* Hentz 1847, $n = 1$, *Clubiona* sp., $n = 3$; Philodromidae, *Philodromus rufus* Walckenaer 1826, $n = 3$ and *Philodromus* sp., $n = 1$. The principal understory species, *E. ovata*, comprised 96% of the total collection, and weighted guild composition in favor of web spinners (98%).

One hundred twenty-four specimens were recovered from white ash and were represented by the Theridiidae, *Theridion murarium*

Table 2.—Results of ANOVA (2 × 2 factorial) for main effects (crown level, branch position) and interaction effects (crown level *vs* branch position) for spider densities on sugar maple at Tully, Cortland County, New York, 1995. 1 = mid-crown *vs* lower crown; 2 = basal branch section *vs* distal branch section; 1, 2 = interaction of crown levels and branch position. Significance (α = 0.05).

Variable	Effects	Spiders/25 Leaf-clusters		Spiders/100 g Leaf weight	
		P	F	P	F
Total Spiders	1	0.45	0.59	0.21	1.70
	2	0.38	0.79	0.36	0.88
	1, 2	0.12	2.43	0.36	0.85
Web Spinners	1	0.40	0.73	0.37	0.84
	2	0.20	1.69	0.16	2.09
	1, 2	0.76	0.09	0.76	0.09
Hunters	1	0.31	1.04	0.31	1.04
	2	0.35	0.88	0.43	0.63
	1, 2	0.06	3.73	0.02	6.43

Emerton 1882, $n = 1$; Linyphiidae, *Ceraticelus* sp., $n = 2$; *Drapetisca* sp., $n = 1$; Araneidae, *Araneus* sp., $n = 1$, *Araniella displicata* (Hentz 1847), n = 40; Clubionidae, *Clubiona* sp., $n = 5$; Thomisidae, *Misumena vatia* (Clerck 1757), $n = 1$; Philodromidae, *Philodromus rufus* Walckenaer 1826, $n = 42$; Salticidae, *Pelegrina proterva* (Walckenaer 1837), $n = 29$ and *Pelegrina* sp., $n = 1$. Spider density on white ash averaged 2.6 ± 1.3 (SE)/100 g of leaf weight. Only 4 (0.03%) individuals were adults; most were juveniles of *P. rufus* and *Araniella displicata* (Hentz 1847). *Philodromus rufus* accounted for 34% and *A. displicata* 32% of the total spiders collected from white ash. Densities per 100 g of leaf weight for these two species were 39% and 30%, respectively. Hunters were the dominant foraging guild on white ash, both in terms of total specimens (63%) and numbers/100 g of leaf weight (60%).

White ash averaged significantly fewer ($t = 2.184$, $P = 0.03$, df = 58) spiders per 100 g of foliage biomass (2.6 ± 1.3) than sugar maple (14.2 ± 0.6). Sugar maple branches (1 m long) averaged 53.3 ± 3.3 g of leaf weight compared to 71.7 ± 7.1 g for white ash ($t = 2.452$, $P = 0.02$, df = 58) branches of the same length. However, sugar maple had significantly ($t = 8.031$, $P = 0.0001$, df = 58) more leaves per 1 m branch (276.8 ± 17.9) than white ash branches of the same length (93.9 ± 10.5 leaves). Each white ash leaf consists of 5–9 leaflets, which most likely accounts for the greater average leaf weight.

Only 712 spiders were recovered while sampling sugar maple foliage yearly from 1975–1995. The collection represented 12 families, 27 genera and 40 species (Table 4). Most were adults (455 or 64%). Numerically dominant families were Salticidae (32%), Philodromidae (21%) and Theridiidae (12%). The salticid *Pelegrina proterva* (Walckenaer 1837) (25%) was the primary species recovered. Hunters were the dominant foraging guild, accounting for 64% of the collection.

Table 3.—Mean (±S.E.) number of spiders/100 g of leaf weight for two branch positions in the mid- and lower crown of sugar maple (n = 10 trees), Tully, Cortland County, New York, 1995.

Spider group	Branch position	Crown level		Crown levels combined
		Lower	Middle	
Webspinners	Basal Half	10.7 ± 8.1	2.1 ± 0.9	6.4 ± 4.1
	Distal Half	6.9 ± 5.0	0.9 ± 0.6	3.9 ± 2.5
	Branch Positions Combined	8.8 ± 4.7	1.5 ± 0.5	—
Hunters	Basal Half	12.1 ± 5.6	10.5 ± 3.2	11.3 ± 3.1
	Distal Half	7.9 ± 3.8	3.0 ± 1.7	5.5 ± 2.1
	Branch Positions Combined	10.0 ± 3.3	6.8 ± 2.0	—

The ability to estimate population densities of arboreal spiders is important for assessing the dynamics of spiders as predators of folivores in forested ecosystems. To determine the relationships between certain tree characteristics and leaf-cluster numbers, Allen (1976b) conducted a dimension analysis of sugar maple in Tully, New York (Cortland County). A leaf-cluster (all leaves derived from a single bud) is the unit of habitat occupied by many insect folivores and spiders. He found that the total number of leaf-clusters/tree can be estimated by dbh^2 or, a combination of tree diameter, height and crown size (length, width). For example, in two separate samples (1970, $n = 18$ trees; 1971, $n = 16$ trees) there was a significant positive correlation ($r = 0.90$, 1970; $r = 0.93$, 1971) between dbh^2 and the total number of leaf-clusters for overstory sugar maples 18–38 cm in diameter. Using a regression derived from the 1971 sample (Allen, unpub. data) ($Y = 574.6 + 87.6$ dbh^2), a sugar maple 14.5 inches (36.8 cm) dbh contains approximately 18,993 leaf-clusters. Assuming that spider density (spiders/25 leaf-clusters) is similar among overstory sugar maples; total leaf-cluster numbers increase or decrease in a predictable manner relative to tree diameter and 2.6 spiders/25 leaf-clusters was representative of the entire maple crown; then a 36–37 cm diameter sugar maple at Heiberg Forest in 1995 contained approximately 1,975 spiders.

DISCUSSION

Previous investigations of spiders associated with forest trees in North America have concentrated mainly on conifers, and have employed a diverse array of sampling methods (Table 5). Relatively few studies have been published on spiders associated with broad-leaved trees. Additionally, spider guild ratios have been based on total number collected, not on population numbers or densities expressed as number per unit of habitat (e.g., spiders/leaf-cluster, spiders/100 g foliage). To be most meaningful, sample ratios of spider guilds should reflect the percent of the estimated total per specific unit. For example, if for the 1995 study the ratio of hunters (65%) to web spinners (35%) is based on total spiders collected, the result is approximately 2:1 in favor of hunters. However, a ratio determined on the basis of spiders/per 100 g of leaf

weight approximates a 1:1 ratio (hunters 56% and web spinners 44%) and more accurately reflects the relative abundance of these two groups per unit of habitat. Employment of different sampling protocols (e.g., timing, technique) and field conditions, however, may have favored one guild over another (Green 1999).

In the 1995 study, the numerically dominant species on both white ash and sugar maple was the hunter *P. rufus*. This arboreal species does not construct a web, but spins a silken retreat on the underside of a leaf for egg laying. Observations of *P. rufus*, both in the lab and under field conditions, indicated that it is extremely fast and agile compared to other spiders encountered. Although *P. rufus* has limited eyesight (Haynes & Sisojevic 1966), agility and swiftness of movement may contribute to its dominant status. These characteristics enhance predator avoidance, prey capture and protection of eggs. This widely distributed species and three subspecies have been recovered from a variety of coniferous and broad-leaved trees in North America (all references Table 5).

The web spinner *E. ovata* was the most abundant species recovered from understory foliage and comprised 96% of all spiders collected in this stratum. Interestingly, this theriidid was also second in abundance on sugar maple overstory (30%). Previous studies of the araneofauna associated with trees do not report *E. ovata* as a common species (all references Table 5). Reillo and Wise (1988) noted that *E. ovata* frequently occurred on weedy vegetation in Maine. Most likely introduced from Europe (Levi 1957), this species (previously described as three separate species of *Theridion*) has three phenotypes (Kaston 1948). Two forms have red markings on the abdomen, while one form is without red markings. In the 1995 study, only three individuals had red markings in the combined overstory/understory collection ($n = 887$).

Typically, *E. ovata* attaches silken lines to a leaf, draws the threads together and partially folds the leaf. Potential prey enter the fold and, in doing so, get caught in the web. The folded leaf and web are comparable to a hunting spider's retreat. Presumably, the folded leaf provides protection from adverse weather, affords a safe haven for egg laying, and facilitates concealment from predators. Five egg

Table 4.—Families, species and numbers of spiders collected on sugar maple foliage from 1975 through 1995, various localities, northern New York State.

Spider taxa	Number of individuals
Dictynidae	
Emblyna manitoba Ivie 1847	1
E. maxima (Banks 1892)	37
E. sublata (Hentz 1850)	22
Emblyna sp.	12
Amaurobiidae	
Callobius bennetti (Blackwall 1846)	1
Coras sp.	1
Theridiidae	
Enoplognatha ovata (Clerck 1757)	1
Enoplognatha sp.	1
Theridion differens Emerton 1882	3
T. frondeum Hentz 1850	50
T. murarium Emerton 1882	19
T. sexpunctatum (Emerton 1882)	1
Theridion sp.	9
Theridula opulenta (Walckenaer 1841)	1
(family only)	2
Linyphiidae	
Ceraticelus atriceps (O.P.-Cambridge 1874)	3
C. emertoni (O.P.-Cambridge 1874)	2
Helophora insignis (Blackwall 1841)	3
Hypselistes florens (O.P.-Cambridge 1875)	1
Neriene radiata (Walckenaer 1841)	1
(family only)	16
Araneidae	
Araneus marmoreus Clerck 1757	18
Araneus sp.	29
Araniella displicata (Hentz 1847)	1
Araniella sp.	13
Cyclosa conica (Pallas 1772)	1
(family only)	7
Tetragnathidae	
Tetragnatha elongata Walkenaer 1841	1
Agelenidae	
Agelenopsis utahana (Chamberlin & Ivie 1933)	3
Clubionidae	
Clubiona canadensis Emerton 1889	7
C. obesa Hentz 1847	14
C. pygmaea Banks 1892	6
Clubiona sp.	22
(family only)	12
Liocranidae	
Phruotimpus borealis (Emerton 1911)	1
Thomisidae	
Misumena vatia (Clerck 1757)	4
Misumena sp.	4
Misumenops sp.	1
Xysticus sp.	4

Table 4.—Families, species and numbers of spiders collected on sugar maple foliage from 1975 through 1995, various localities, northern New York State.

Spider taxa	Number of individuals
Philodromidae	
Philodromus sp. (aureolus group)	3
P. exilis Banks 1892	6
P. rufus Walckenaer 1826	51
P. vulgaris (Hentz 1897)	4
Philodromus sp.	27
(family only)	56
Salticidae	
E. militaris (Hentz 1845)	4
Evarcha hoyi (Peckham & Peckham 1883)	2
Hentzia mitrata (Hentz 1846)	2
Pelegrina flaviceps Kaston 1973	1
P. montanus (Emerton 1891)	19
P. proterva (Walckenaer 1837)	180
Pelegrina sp.	16
Phidippus whitmanii Peckham & Peckham 1990	1
(family only)	5
Total	712

sacs of *E. ovata* averaged 103.0 ± 18.0 eggs/sac, about six times that observed for *P. rufus* (17.2 ± 2.0, $n = 5$).

There were no statistically significant differences ($\alpha = 0.05$) in spider densities between the two crown levels or between the two branch positions sampled on sugar maple (Table 3). This apparent lack of statistical differences results from a combination of low means, high variances and frequent zero counts. We believe, however, the data suggest biological differences and recommend that lower crowns should be sampled to obtain a representative picture of the web-spinning fauna associated with sugar maple foliage. Both the mid- and lower crown should be sampled for hunters. Clearly, future studies should use a larger sample size. Variables such as habitat distribution, differences in microclimate and territorial behavior of some species, for example, affect both inter- and intraspecific distributions. Location preferences were not observed for dominant families, genera, or species. Because analyses were based on densities per 100 g of leaf weight, a distal branch section from either the lower or mid-crown level of sugar maple provides a representative sample of the dominant spider taxa present.

Our sample of only 5 white ash trees ($n = 80$ branch positions) provided estimates of spider density per 100 g of leaf weight and information on species composition. The sample was not large enough, however, to provide insight about the within-crown distributions of spider taxa. For total spiders, variances were homogeneous, but there were no significant differences ($P > 0.05$) between crown or branch positions.

There were significantly fewer spiders/100 g of leaf biomass on white ash compared to sugar maple. Sugar maple had a higher average number of leaves per meter of branch length (276.8 ± 17.9) compared to the average number of leaves (each leaf with 5–9 leaflets) on white ash (93.9 ± 10.5), but lower leaf biomass. Gunnarsson (1990) found a positive correlation between spider abundance and density of spruce needles. Similarly, Hatley and MacMahon (1980) noted that both spider numbers and density increased when they tied branches of sagebrush together, thereby increasing foliage density. Despite lower leaf biomass, the more dense or clustered arrangement of sugar maple leaves per unit of branch length, compared to white ash, may account for the greater abundance of spiders on sugar maple branches. For both web-

Table 5.—Examples of foraging-guild composition (web spinner vs hunter) reported for arboreal spiders in North American forests, orchards and plantations.

References	Tree species	Percent of individuals by guilds	Sampling method
Dahlsten et al. 1977	white fur	64% web 36% hunt	unknown
Dondale 1956	apple	62% web 38% hunt	mostly tapping branches, some hand collecting and fumigation
Halaj et al. 1996	Douglas-fir	web dominant coastal, hunt dominant inland	beating branches, lower canopy
Jennings 1976	black walnut plantation	14% web 86% hunt	hand collecting from the ground
Jennings & Diamond 1988	balsam fir spruces	slightly more web	pole pruner with catchment basket; branches lowered, cut, and bagged
Jennings & Collins 1987	red spruce	54% web 46% hunt	pole pruner with clamping device, cut and dropped onto ground cloth
Jennings et al. 1990	balsam fir, red spruce	68% web 32% hunt	pole pruner with catchment basket; branches cut, lowered and bagged
Mason 1992	Douglas-fir, true firs	hunt dominant one site, web dominant second site	beating branches
Mason et al. 1997	Douglas-fir, grand fir	47.3% web 52.7% hunt	pole pruner with catchment basket, branch beaten in plastic drum
Renault & Miller 1972	fir, spruce	web dominant	shook branch after it was cut and fell to ground
Pettersson 1996	spruce	web dominant >97%	branch cut, lowered and bagged
Uetz & Dillery 1969	maple	web dominant	lower branches examined while investigators stood on the ground

building and hunting spiders, habitat structure greatly influences spider location (Robinson 1981). Leaf density arrangement may be critically important by providing better habitats for prey, providing protection from predators, providing favorable microhabitats (Almquist 1970), and presenting more suitable structure for behavioral activities such as web or retreat building (Stevenson & Dindal 1982).

For sugar maple, spider-guild composition was similar between studies. The 20-year collection consisted of 36% web spinners and 64% hunters; the 1995 study, 35% web spinners and 65% hunters. These consistent values clearly demonstrate dominance of the hunter guild on foliage of overstory sugar maple. Our guild-composition results differ markedly from that found on coniferous foliage (Table 7), where web spinners dominate. In the 20-year study, species of *Pelegrina* were the most abundant group recovered from sugar maple. More commonly referred to as jumping spiders, salticids are noted for their large specialized anterior median eyes which give them superior eyesight compared to other spiders (Jackson & Pollard 1996). Unlike *Philodromus rufus* (dominant in the 1995 study), a hunter with relatively poor vision, salticids (including *Pelegrina proterva*) may have an advantage when ambushing prey. Previously, *P. proterva* has been found on black walnut, *Juglans nigra* L.; balsam fir, *Abies balsamea* (L.) Mill.; white pine, *Pinus strobus* L.; loblolly pine, *P. taeda* L.; shortleaf pine, *P. echinata* Mill.; common persimmon, *Diospyros virginiana* L.; peach, *Prunus persica*

Batsch (Jennings 1976); apple, *Malus* spp.; (Dondale 1956) and spruces, *Picea* spp. (Jennings & Dimond 1988).

The 20-year collection was examined prior to the 1995 study and, consequently, we predicted that *Pelegrina proterva* would be common among the more intensive samples taken at Heiberg Forest. However, this species accounted for only 0.5% of the total collection in 1995. Undoubtedly, many factors influenced spider abundance, composition and diversity in both collections. For example, in the long-term survey sugar maple branches were clipped with pole pruners and allowed to drop. Although most of these samples were caught before hitting the ground, spiders of both guilds could easily have been lost. Lost specimens may, in part, explain the similarity in total spiders collected in the two studies. Also, the 1995 collection took place throughout the growing season, whereas 1975–1995 sampling occurred during a very narrow time frame. Despite the large difference in sample sizes ($n = 40$ branches, 1-yr study; $n = 3,000$ branches (150/yr), 20-yr study), 694 individuals were obtained in 1995 (Table 1) and 712 in the 20-year collection (Table 4). Nonetheless, the 20-yr study yielded more species of spiders than the 1-yr study, as might be expected. In shrub (e.g., Hatley and MacMahon 1980), agricultural crop (Sunderland and Samu 2000) and forest (e.g., Stratton et al. 1979) communities, spider species composition can be significantly altered with changes in habitat structure. Alteration of structure affects habitat heterogeniety and microclimate, both of which play major roles in determining the composition of spider communities (Post & Reichert 1977). The northern hardwood stands that were sampled annually for two decades changed visibly in terms of canopy density and crown size over time. Typically, crowns in most northern hardwood stands tend to close with increasing stand age and a natural stratification of crowns occurs due to unequal growth rates and genetic differences (Nyland 1996). It is reasonable to assume the microclimate throughout the canopy and within individual crowns, and crown structure as a habitat for spiders, would change as well. Another factor that may have contributed to lower spider diversity in 1995 compared to the 20-year collection is that the two regions occur in different geographic provinces, even

though the study sites were only 140–180 km apart. Spider community structure and composition in forested communities vary with changes in geographic location and in different biotypes. This may occur even though the composition of these plant communities is similar, the locations where sampling occurs exist within a relatively small geographic area and locations are sampled on the same date (Renault & Miller 1972; Halaj et al. 1996). The two sample locations in the present study occur in two different broad ecological provinces; that is, climatic subzones controlled mainly by continental weather patterns (Bailey et al. 1994). At a larger scale, these locations also represent quite different forest ecosystems based on soils, topography, local weather, land use history and elevation. The site used in 1995 is located in the Northeast Appalachian Zone and the long-term study took place in the Western Adirondack and Adirondack Foothills zones (Stout 1958).

It is unlikely spiders, either singly or as a collection of species, have the type of predatory response capable of preventing outbreaks of folivores in forest or orchard ecosystems. They may play an important role, however, as regulators when pest populations are sparse (Renault & Miller 1972; Miliczky & Calkins 2002)). Knowledge of spider habits and requirements (Uetz 1991) have reached a level where it may be possible to enhance their pest control potential by maintaining or creating more suitable habitats; that is, by taking a "conservation" approach to biological control (sensu DeBach 1964). Additional work on spider diversity and ecological requirements in northern hardwood stands with differing geographic locations, dissimilar species composition and variable tree age class distributions may provide the ecological background needed to enhance the role of these predators in the natural control of certain forest pests.

For total spiders, dominant taxa and web spinners, within-crown distribution analyses indicated no significant habitat selection by spiders for either mid- or lower crown strata or for basal or distal portions of sugar maple branches. However, significantly fewer hunters were found in distal portions of mid-crown sugar maple branches. The dominant species on both overstory sugar maple and white ash overstory in the northern hardwood stands studied was *Philodromus rufus*. White ash had

fewer spiders and fewer species of spiders/100 g leaf weight compared to sugar maple. Understory foliage was dominated by *Enoplognatha ovata*, and this species was also the second most abundant spider on sugar maple overstory.

Unlike spider-guild composition of some conifers, more hunters than webspinners occurred on both sugar maple (hunters 65%, web spinners 35%) and white ash (hunters 63%, web spinners 37%) in 1995. For this intensive study, *Philodromus rufus* was the dominant hunter. The 20-year collection from sugar maple foliage in northern New York also indicated that hunters (64%) dominated, but in this sample *Pelegrina proterva* as the most common species recovered.

For future studies of arboreal spiders on broad-leafed trees, our results indicate that an intensive sampling protocol (i.e., larger sample within trees, branches cut and lowered) be employed for more than one season.

ACKNOWLEDGMENTS

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